On the nature of the gated colour opponency in the ON-units of the frog retina: electrophysiological study and model

Elena M. Maximova, Vadim V. Maximov and Oleg Y. Orlov

Institute for Problems of Information Transmission,
Russian Academy of Sciences, 101447 Moscow, Russia

Abstract. Ganglion cells of the ON-type in the frog retina produce colour-dependent responses differing in temporal patterns (short burst to excitation of red-sensitive cones as opposed to prolonged discharge if blue-sensitive 'green rods' are excited). Their gated colour opponency (Kicliter et al., 1981 Brain Research 210, 103-113; Maximov et al., 1985 Vision Research 25, 1037-1049) becomes apparent from the OFF-responses in conditions when the test stimuli are superimposed on a background of another colour. So, when a blue glass is introduced in the light beam (decreasing the excitation mainly of red-sensitive cones), an OFF-response is observed, much like the response to the onset of blue light. It has been suggested that opponency in ON-cells is asymmetric, i.e. that the red signal reaches the blue channel with reversed sign, but not vice versa.

A single-unit-recording study revealed the dependence of ON-cell responses both on the colour of stimuli presented in the centre of the receptive field and on the steady illumination of its surround. Surround illumination was found to favour OFF-responses in ON-units. In some cases even the cessation of blue light elicited an OFF-response with a discharge pattern resembling that of the onset of red light. In these cases the response to introduction of a yellow glass could be observed. These observations prove some degree of symmetry in the opponency of the red and blue channels.

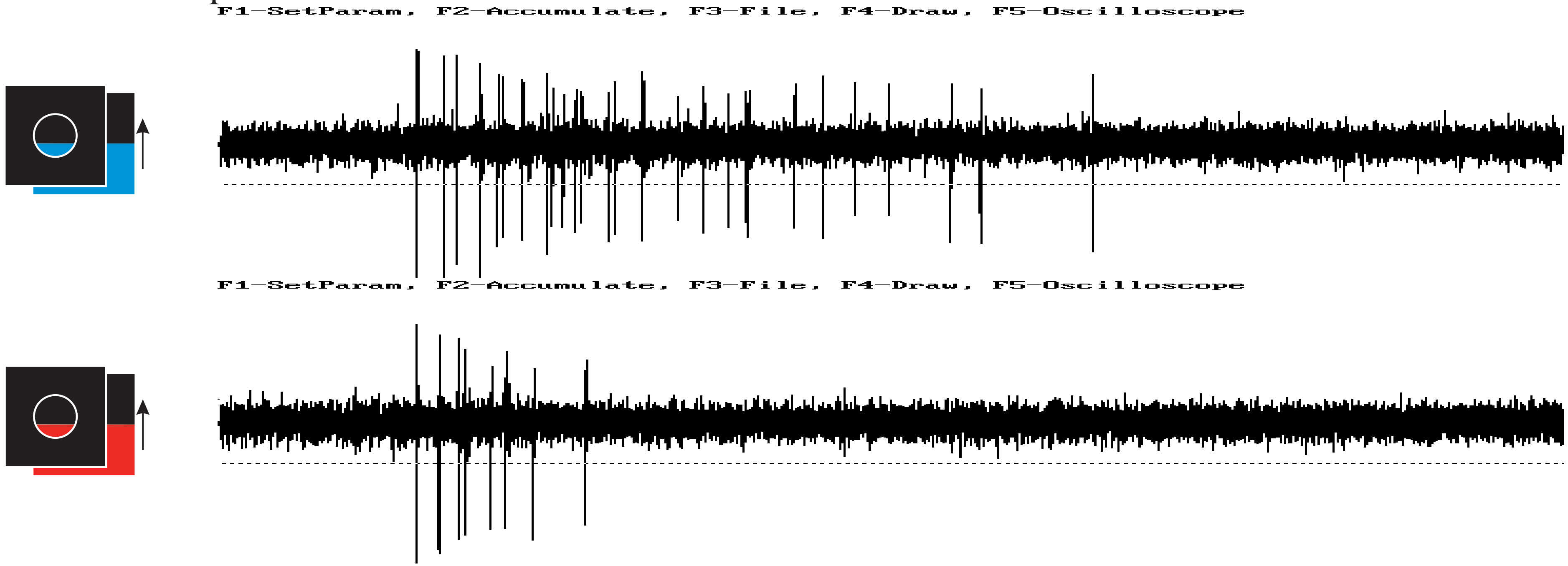
It is suggested that feedback from horizontal cells onto photoreceptor terminals is involved in the gated colour opponency. A circuit model that reproduces the observed phenomena is presented.

[Supported by the RBRF grant 95-04-11824a]

Introduction

In many investigated species possessing colour vision, colour-processing neurons at different levels of visual system demonstrate colour opponency, i.e. excitation of different spectral receptor types elicits responses of opposite signs (i.e., ON vs. OFF, or increase vs. decrease of spontaneous spike rates).
In frogs and toads colour coding retinal ganglion cells respond by ON-discharge to flash or onset of whatever illumination, but the discharge pattern, i.e. the temporal distribution of spikes differs according to relative excitation of receptor spectral types: they respond to red light by short and dense discharge, and to blue light by long and often rhythmically arranged spike train.
But some kind of opponency of input signals does exist in ON-units:

- an addition of red light to blue one (increasing the stimulus intensity) diminishes ON-response,
- an introduction of blue glass into a light beam (decreasing the intensity of the light) elicits an OFF-response.



A prolong response of the ON ganglion cell to blue stimulus (upper trace) and a short one to red stimulus (lower trace) entering the centre of the receptive field (RF).

Previous models

Kicliter, Kay & Chino (1981) suggested that the colour processing at stages previous to the ON-unit was distributed among two separate channels directly exciting the ON-unit:

- the channel connected to green rods was colour opponent - a long-wavelength signal suppressed a short-wavelength induced activity,
- the channel directly connected to red-sensitive cones was non-opponent.

The model did not represent a specific anatomical circuit.

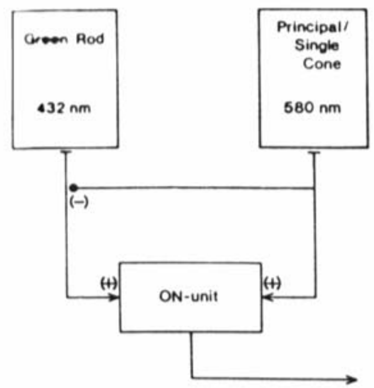


Fig. 6. A model which could account for the response characteristics of spectrally opponent ON-units.

and Virtanen[23]. The other feature of the model is that the P580 channel gates activity in the P432 channel. This is based on the spectral limits of the inhibitory effect shown above and is in accord with Reuter's[22] proposal. The model provides an explanation for the fact that a stimulus composed of both short and long wavelength light produced a

Maximov, Orlov & Reuter (1984) gave concrete expressions to the model.

An important feature of the opponent channel was that a sustained stimulation of the green rods controlled the OFF-response to red stimulus:

- the red OFF-response did not pass (was gated) if the green rods were not stimulated,
- but the same decrease in the stimulation of red-sensitive cones, superimposed on a steady background of blue light, produces an OFF-discharge..

What is the difference between the strong blue-sensitive input to the On ganglion cells projecting to

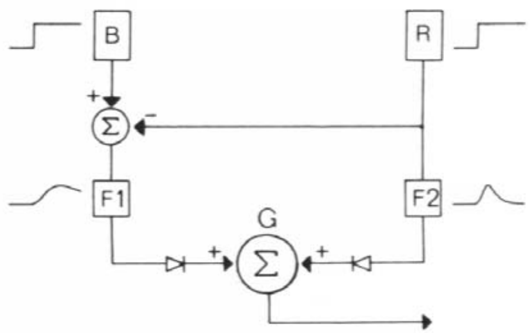
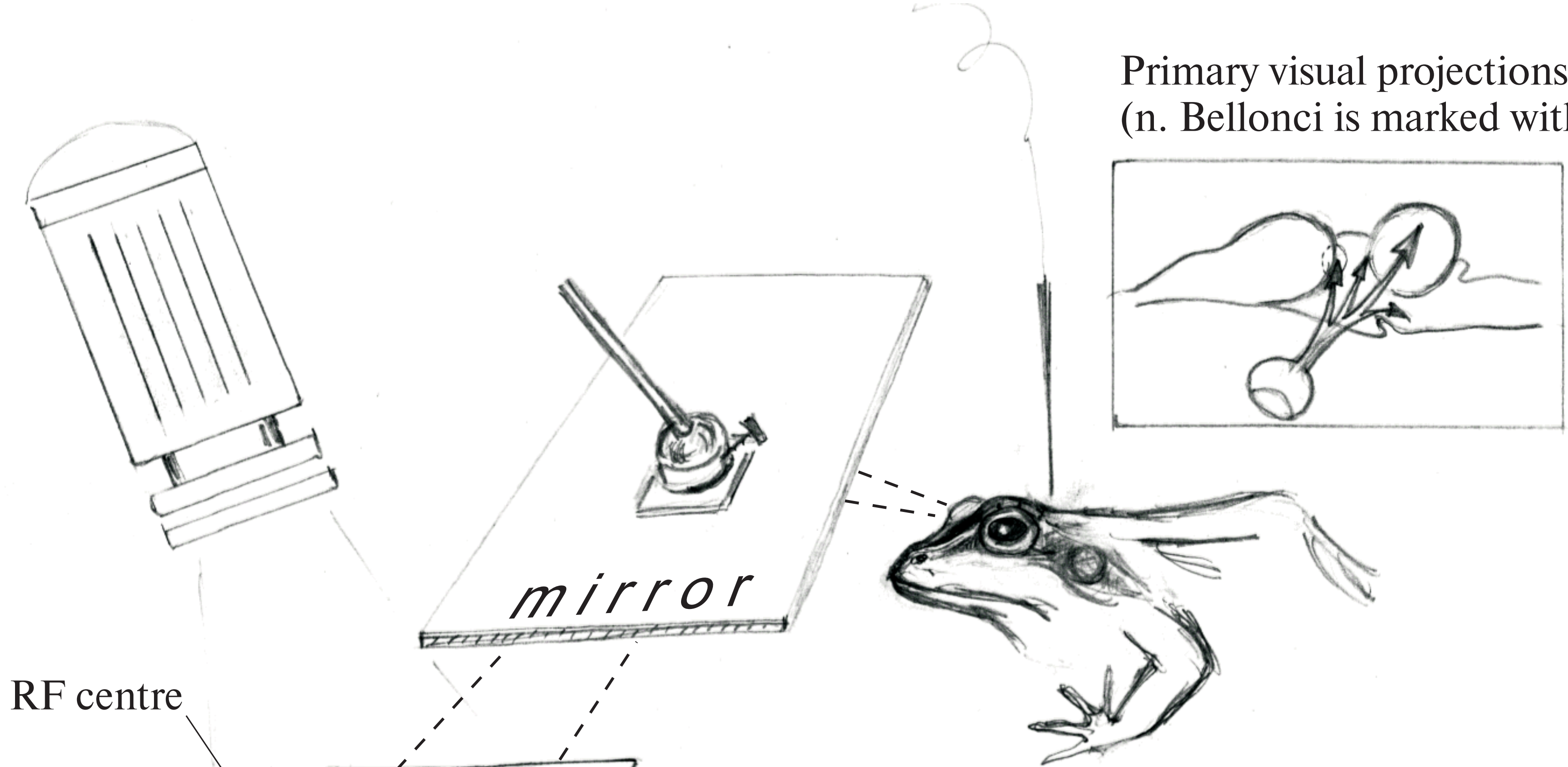


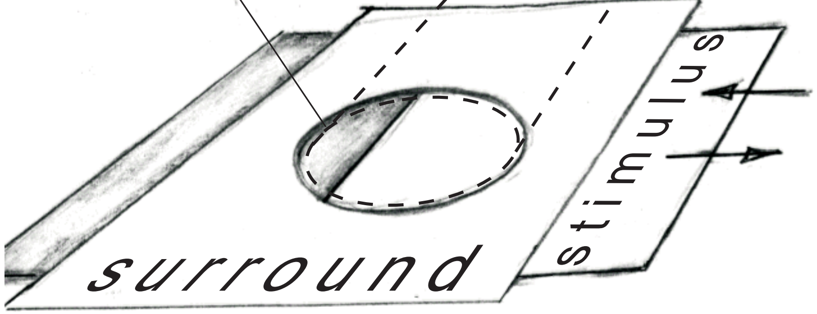
Fig. 8. Qualitative network model to account for the described response characteristics of the receptive field centre of a Bellonci On-unit. The On ganglion cell (G) sending its axon to the neuropil of Bellonci receives rectified inputs from blue- (B) and red-sensitive (R) receptors. The curves associated with the electronic filters F1 and F2 show how these filters distort the responses to step stimulations of B and R respectively. R is subtractively connected with the blue-sensitive channel at a point preceding F1 and F2, and thus R-signals depress B-signals when both receptor types are simultaneously stimulated. Further a relative *decrease* in the stimulation of R, combined with sustained B-stimulation, produces a response indistinguishable from the response to increased B-stimulation.

Methods

Responses of retinal ON-type ganglion cells were recorded from their axonal terminals in nucleus Bellonci (dorsal thalamus) of frogs *Rana temporaria* and *R. ridibunda*.

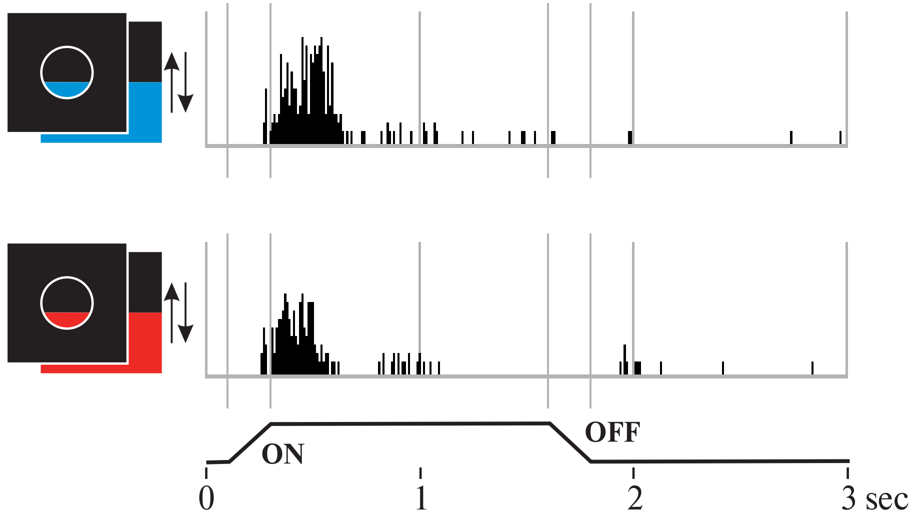


Primary visual projections in the frog (n. Bellonci is marked with colour)



The receptive field centre of a unit was mapped by flashing light spot or moving white paper on the black background. Stimuli (sheets of coloured papers) were moved with a constant velocity across the RF centre on a velvet-black background, the RF surround being covered with a white or black screen.

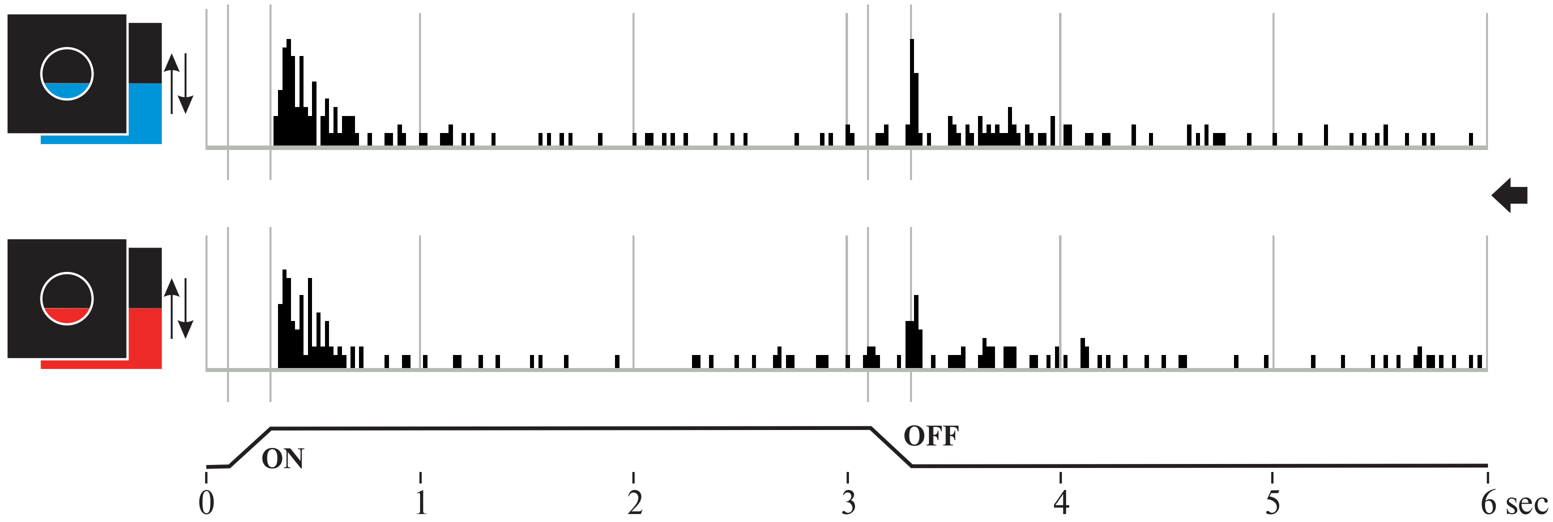
Results



Poststimulus histograms of the ON-unit responses to blue and red stimuli moving in the RF centre. Small OFF-response can be seen to red stimulus.

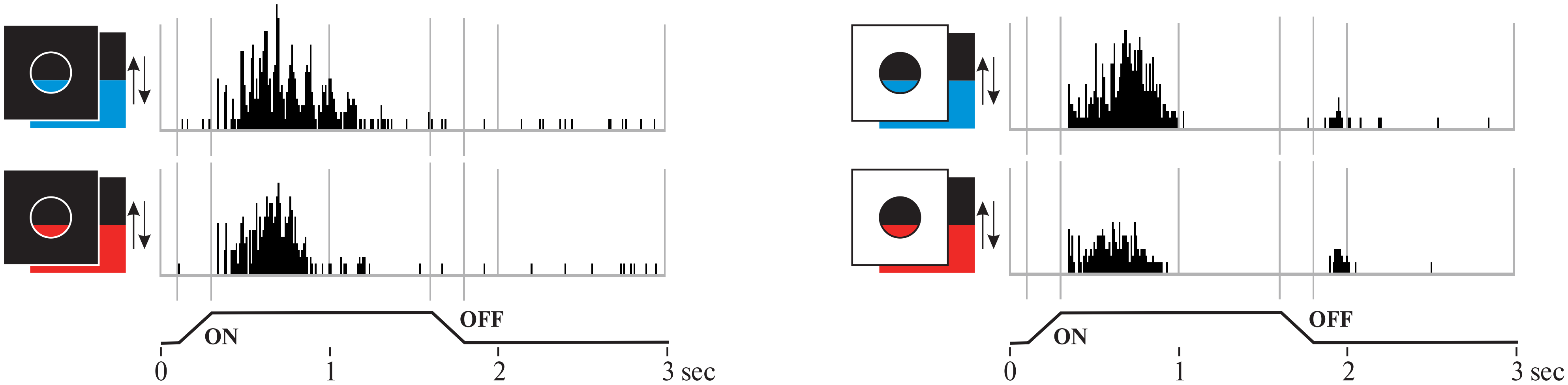
The detailed investigation using accumulation of cell responses to stimuli presented in the RF centre, provided the RF surround was not illuminated, permitted us to see several ON-units that discharged not only when stimulus entered its RF centre, but when it left it too. These OFF-responses were elicited both by blue and red stimuli and were always considerably smaller than ON-responses. Steady illumination of the RF surround (covering with a white screen) enhanced the OFF-responses, or revealed them if they were absent in a dark surround. In some case OFF-responses occurred also when yellow glass (not only blue one) was introduced in a light beam. In the framework of the proposed schemes these phenomena suggest:

- sometimes one colour channel failed to gate the other,
- the colour opponency should exist in the red channel too.

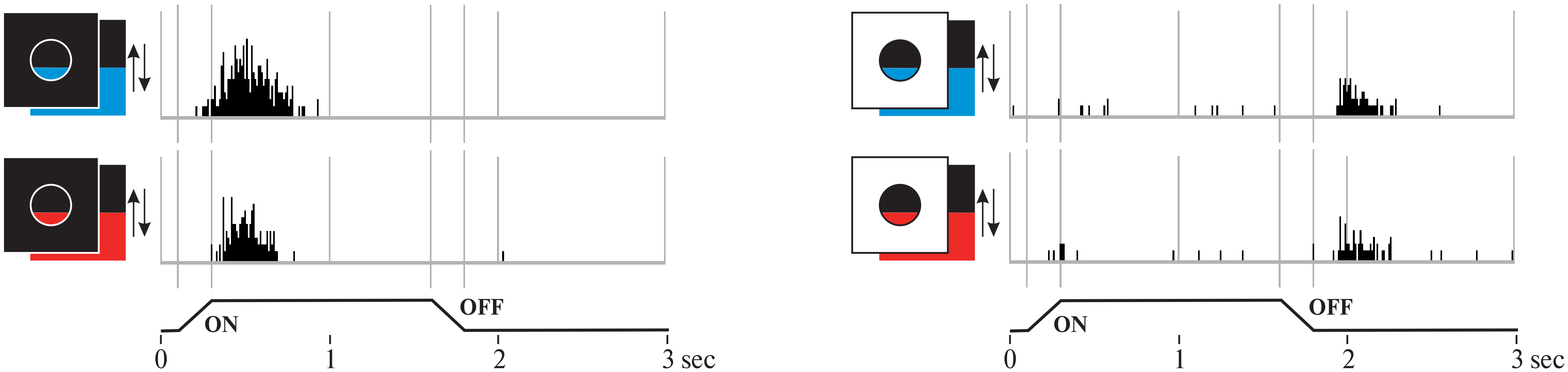


The OFF-responses of this On-unit are more pronounced both to blue and red stimuli.

Steady illumination of the RF surround favours OFF-responses to stimuli moving in the RF centre.



Poststimulus histograms of the ON-unit responses in different conditions of stimulation.
Note the absence of OFF-responses when the RF surround is black.
White surround slightly inhibited ON-responses and revealed OFF-responses.

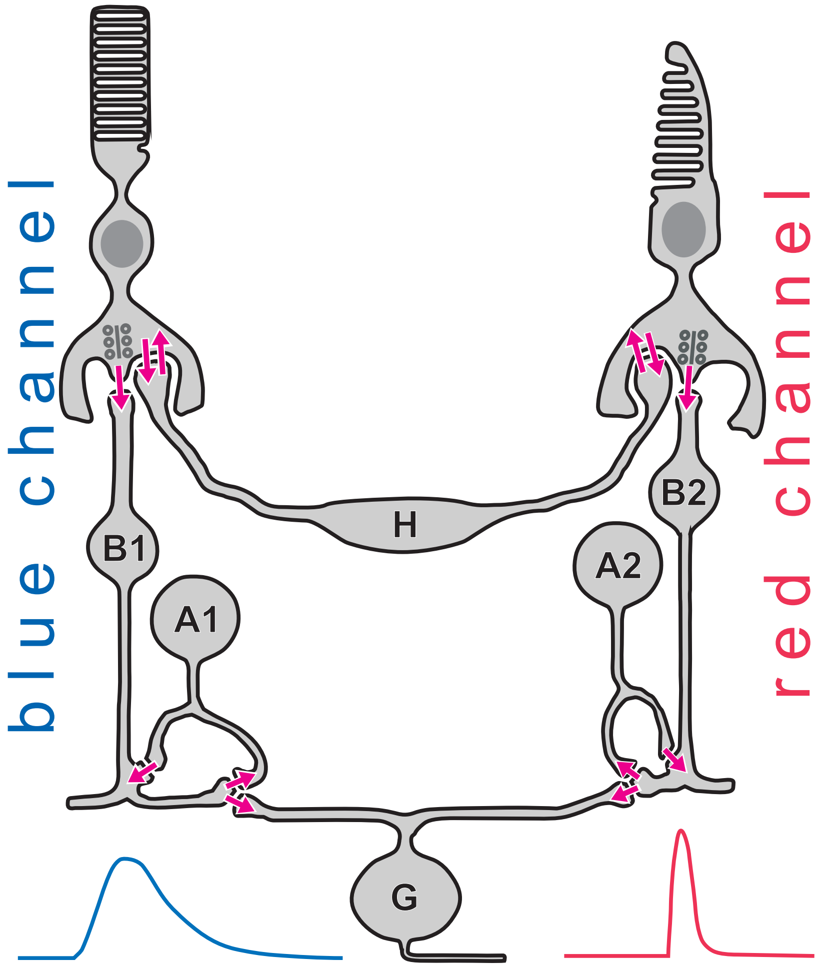


In this case white surround completely inhibited ON-responses and revealed pronounced OFF-responses..
Thus, the pure ON-unit (with black surround) was "transformed" into the pure OFF-unit.

The Model

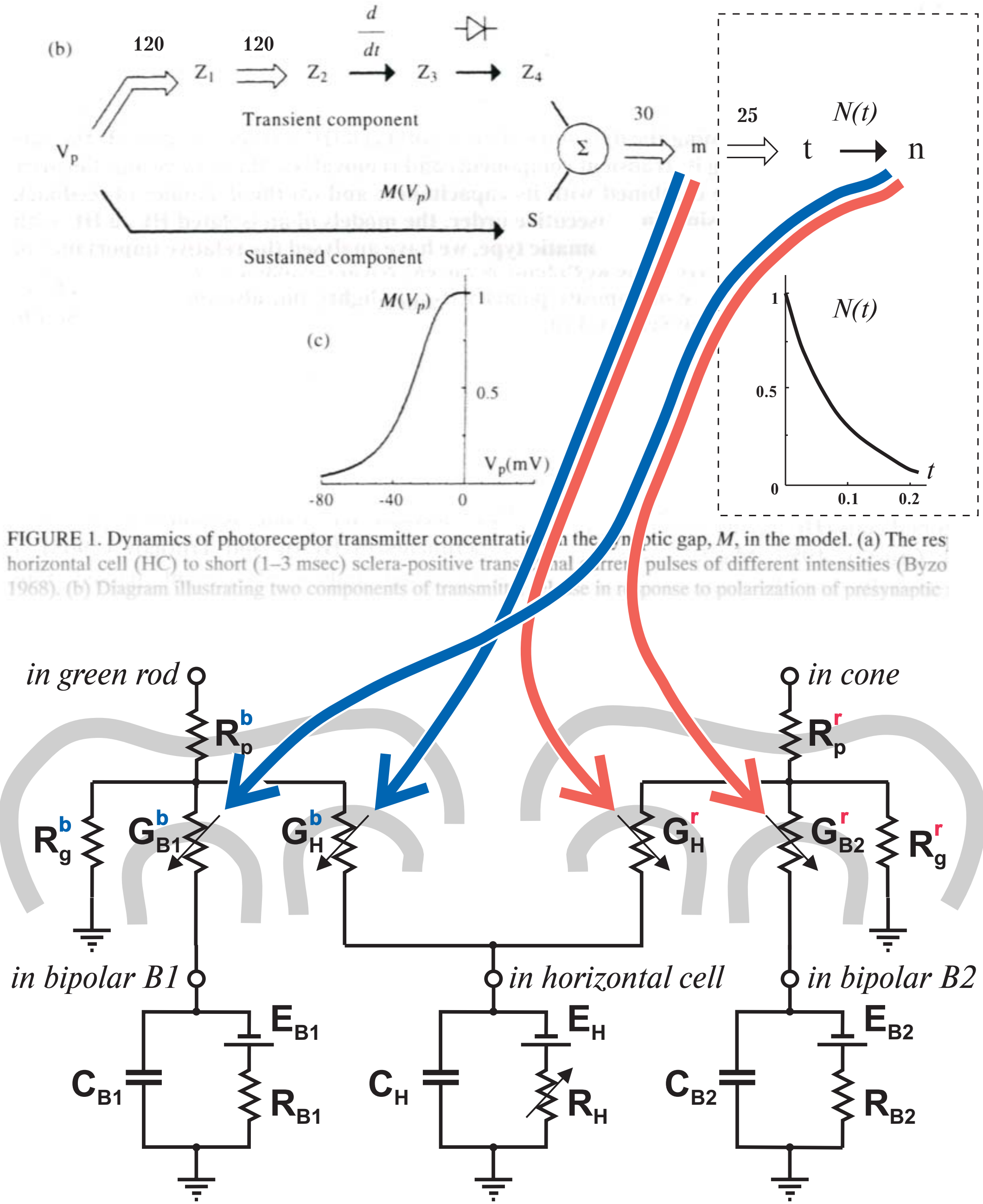
It is supposed that:

- the main channels conducting signals to the ON-type ganglion cell (**G**) are depolarizing bipolars of two types:
  - the **blue channel** - bipolars (**B1**) connected to short-wavelength sensitive receptors (green rods and/or blue-sensitive cones, if any),
  - the **red channel** - bipolars (**B2**) connected to long-wavelength sensitive cones;
- the tonic opponent interaction of colour signals is mediated by horizontal cells (**H**) in the outer plexiform layer;
- it being assumed that this interaction is reciprocal:
  - the red signal is subtracted from the blue one in the green rod synapse,
  - the blue signal is subtracted from the red one in the synapse of red-sensitive cones:
- the gated colour opponency in each channel results from the nonlinear relationship between potentials at the photoreceptor presynaptic membrane and the modelled ON-bipolar response - some rectification at the dark level;



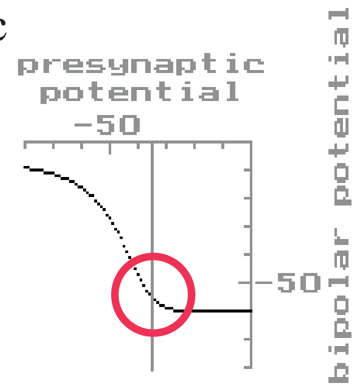
- the last step in the processing of both blue and red signals before they reach the ganglion cell (presumably made by the use of amacrine cells, **A1** and **A2**, in the inner plexiform layer) include:
  - temporal differentiation to get transient responses,
  - low-pass filtering with different rates in blue and red channels reflecting the difference in signal kinetics,
  - signal rectification.

Signal processing in photoreceptor synapses

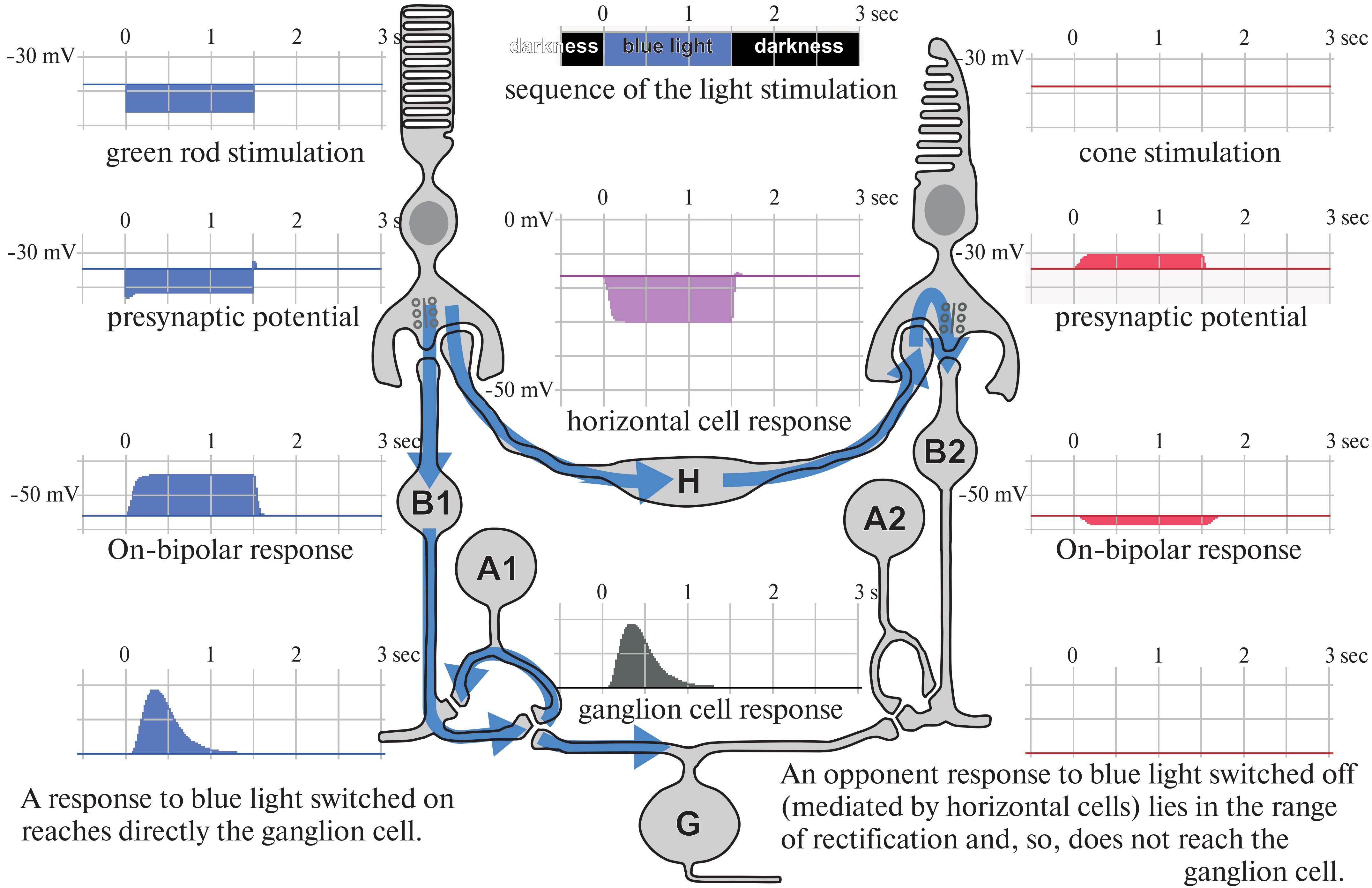


Quantitative model of the signal processing resulting in the gated opponency was compiled from the already existing program modules (Maximov & Byzov, 1996. **Horizontal Cell Dynamics: What are the Main Factors?** *Vision Research*, **36**, No.24, 4077-4087).

The basic scheme of a sign-conserving synaptic connection describing the glutamate release/removal and its influence on the conductance, $\mathbf{G_H}$, of the horizontal cell postsynaptic membrane was supplemented here with a chain of signal transfer in sign-inverting ON-bipolar synapses, following the action of the glutamate. The chain consists of low-pass filter and some function ***N(t)*** reflecting the inverse influence on the concentration, **n**, of second-messanger changing the postsynaptic conductance, $\mathbf{G_B}$. This function together with a saturation near the synaptic reversal potential gives the necessary nonlinearity as can be seen from the plot of the modelled bipolar membrane potential versus presynaptic potential.



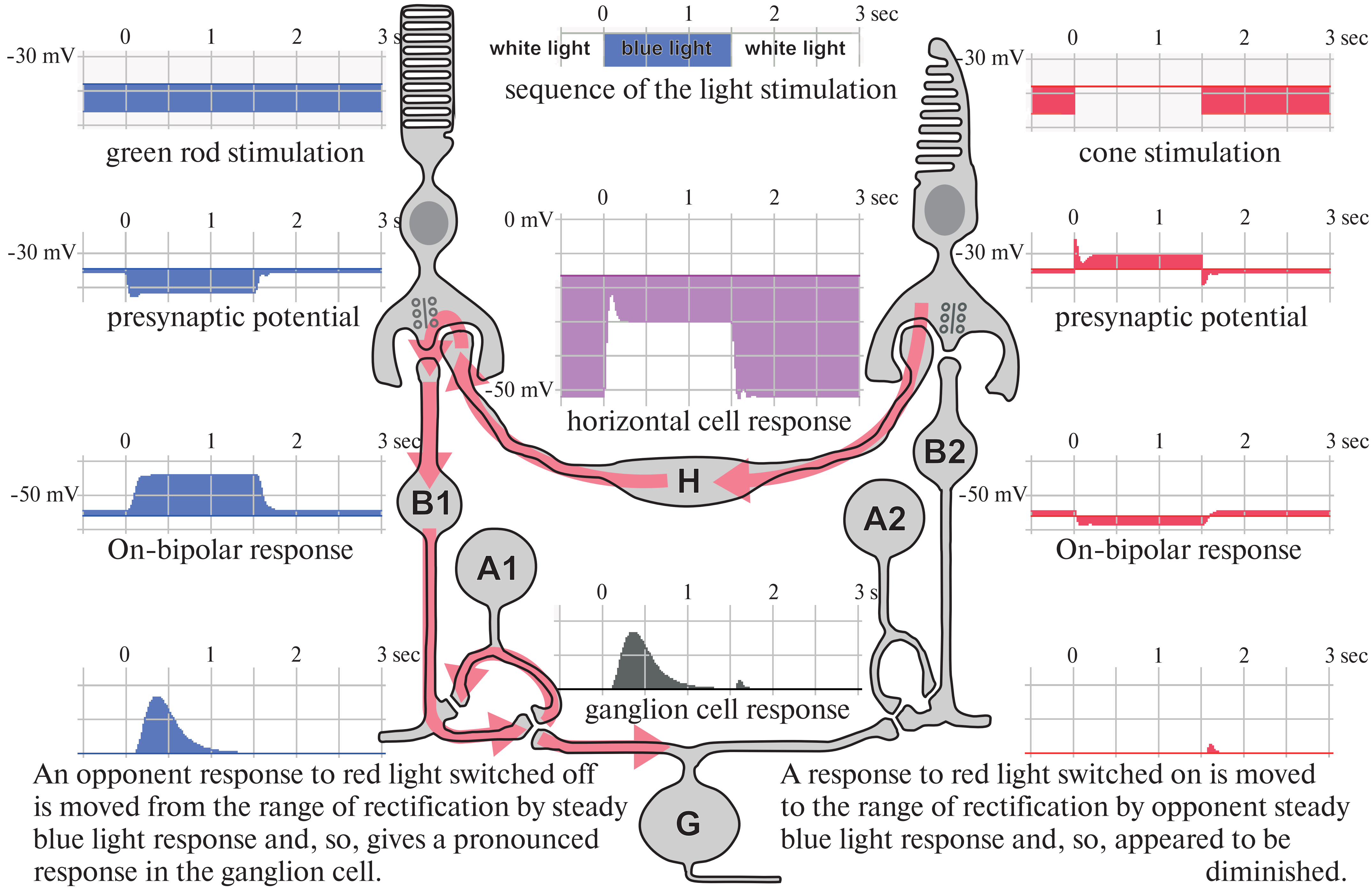
Responses of the model to blue light



A response to blue light switched on reaches directly the ganglion cell.

An opponent response to blue light switched off (mediated by horizontal cells) lies in the range of rectification and, so, does not reach the ganglion cell.

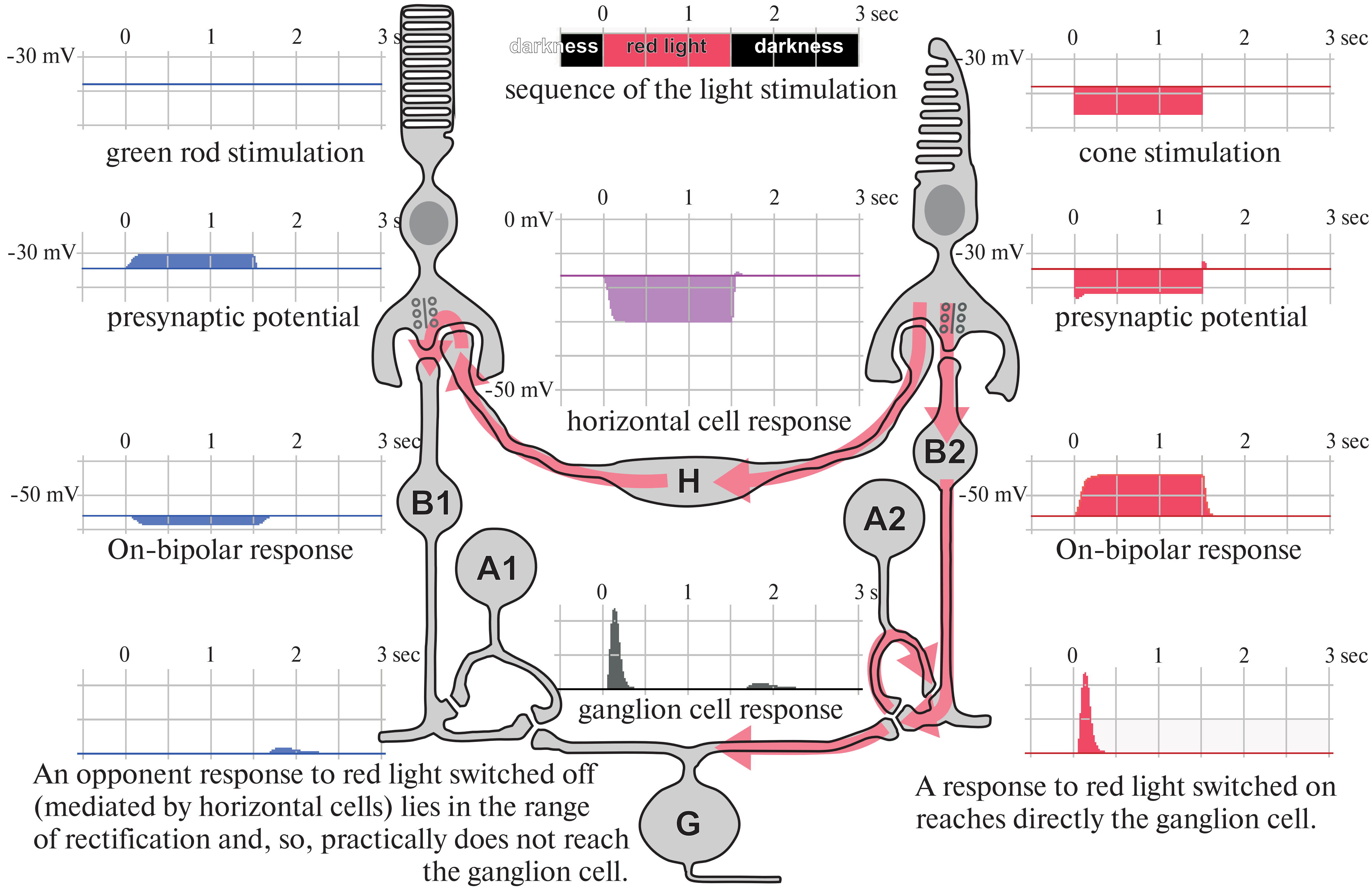
Responses of the model to blue glass introduced in a white light beam



An opponent response to red light switched off is moved from the range of rectification by steady blue light response and, so, gives a pronounced response in the ganglion cell.

A response to red light switched on is moved to the range of rectification by opponent steady blue light response and, so, appeared to be diminished.

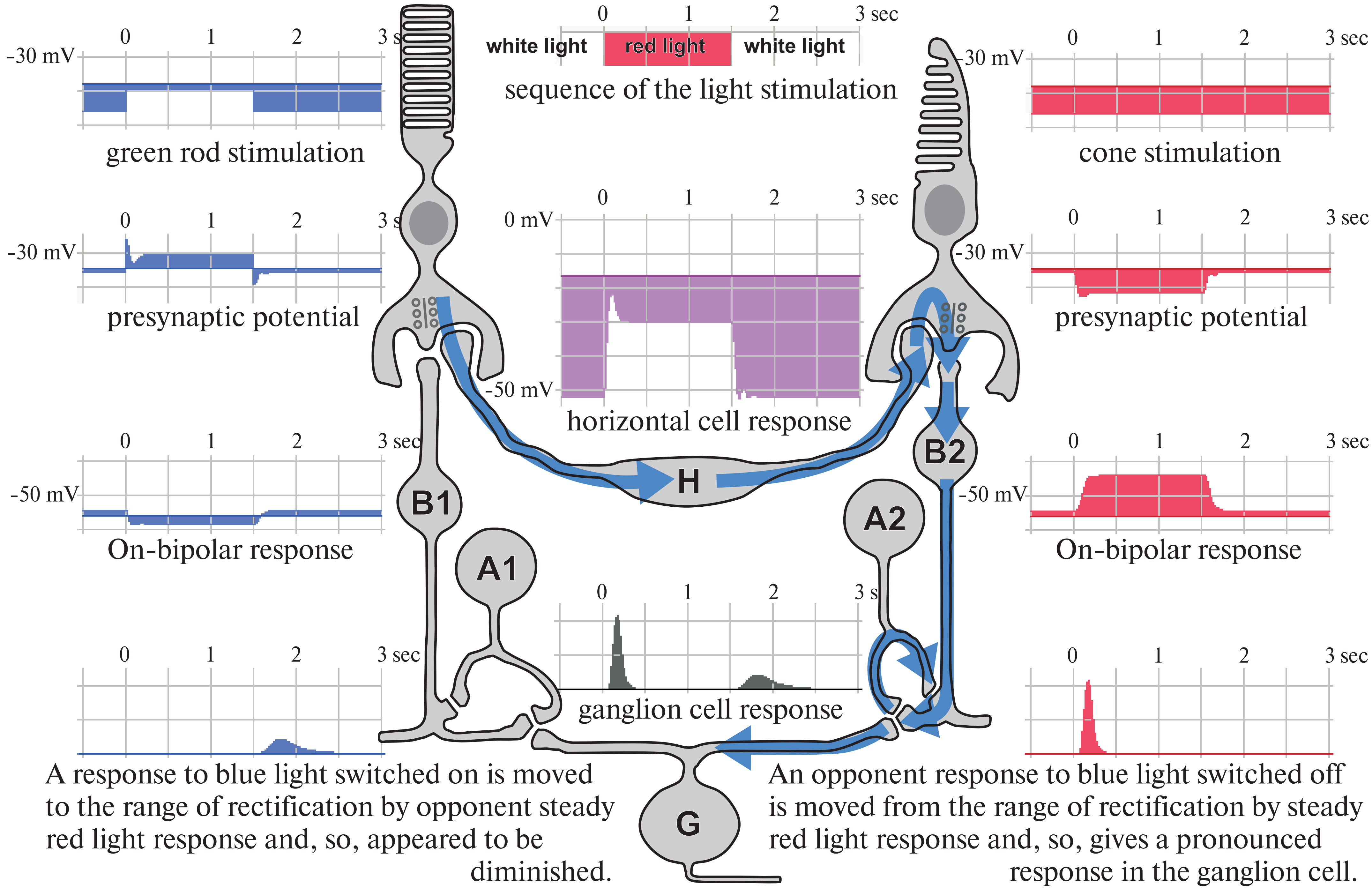
Responses of the model to red light



An opponent response to red light switched off (mediated by horizontal cells) lies in the range of rectification and, so, practically does not reach the ganglion cell.

A response to red light switched on reaches directly the ganglion cell.

Responses of the model to red glass introduced in a white light beam



A response to blue light switched on is moved to the range of rectification by opponent steady red light response and, so, appeared to be diminished.

An opponent response to blue light switched off is moved from the range of rectification by steady red light response and, so, gives a pronounced response in the ganglion cell.